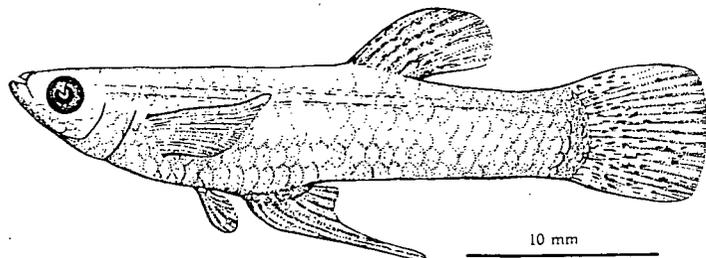
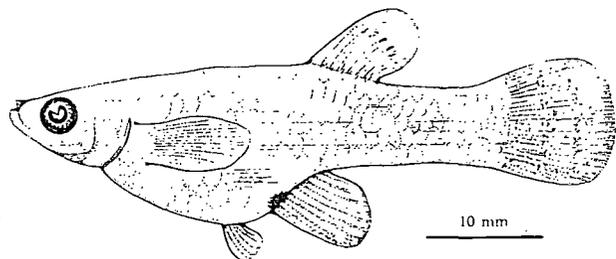


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## Chapter 2 The mosquitofish — a valuable mosquito-control agent or a pest?

L. N. Lloyd, A. H. Arthington and D. A. Milton

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Top: Female (upper) and male (lower) *Gambusia affinis* (redrawn from McDowall 1980, by Ruth Altman); Bottom: A typical mosquitofish habitat.

### Introduction

The mosquitofish, *Gambusia affinis* (Baird & Girard), is a small, live-bearing fish native to central America that has been distributed worldwide as a mosquito-control agent. It is probably the most widely distributed freshwater fish in the world (Krumholz 1948), although rainbow trout, largemouth bass, common carp, grass carp and the Mozambique tilapia are close rivals (Moyle & Cech 1982). *G. affinis* has been established in the wild in Australia since 1925, but has only recently attracted scientific study (see Trendall 1982; Arthington et al. 1983; Arthington et al. 1986; Arthington & Mitchell 1986; Milton & Arthington 1983). This chapter presents a selective review of the world literature on the biology and ecology of *G. affinis*, placing the limited data from Australia in perspective. We evaluate two related questions: is the mosquitofish of value in mosquito control, and is it having an adverse impact on aquatic environments and native fish populations?

### Taxonomy

*G. affinis* belongs to the family Poeciliidae, order Cyprinodontiformes (Rosen & Bailey 1963). The family consists of various live-bearing species from tropical and subtropical regions of the Americas.

The genus *Gambusia* comprises about thirty species, many of which are rare and restricted in distribution (Rivas 1963). *G. affinis*, however, is widely distributed throughout the southern United States and is split into two subspecies, *G. a. affinis*, the western form, and *G. a. holbrooki*, the eastern form. Mosquitofish are small, translucent grey with a bluish sheen on the sides, and have a silvery belly. The fins are colourless with transverse rows of black pigment spots (Sterba 1962), and in males the anal fin is modified to form a long, thin, intromittent organ, the gonopodium (Peden 1972). The body is slightly compressed, with a large and

considerably flattened head, large eyes, and a small terminal mouth (Scott et al. 1974; see frontispiece).

## Distribution

The two subspecies are spatially separated over most of their ranges (Rivas 1963), but intergrades occur where their ranges overlap in southern Alabama and north-west Florida (Krumholz 1948; Black & Howell 1979). In the United States, mosquitofish have been dispersed widely for mosquito control since 1905, now occurring in most mainland states (Krumholz 1948; Lee et al. 1980). The first overseas transfer of *G. affinis* was to Hawaii in 1905 (Seale 1917), and subsequently, mainly during the 1920s, mosquitofish were distributed to many other countries (see figure 2.1 and table 2.1). Most records of transfers do not indicate the subspecies concerned, but, circumstantially, it seems that both were involved.

The introduction of *G. affinis* into Australia is poorly documented, with conflicting reports on the schedule of major introductions (see figure 2.2). Although present in Australia in the early 1920s as an aquarium fish, *G. affinis* was not released for mosquito control until 1925 (Wilson 1960). According to Marshall (1966), Australia, unlike most countries, received its original stocks from Mexico and Texas, where the nominate subspecies is endemic. However, Wilson (1960) reported that Australian stocks were derived from Georgia, USA, where *G. a. holbrooki* is present, via Italy in 1926. Recent examination of populations throughout Australia supports Wilson's claim (Lloyd & Tomasov 1985).

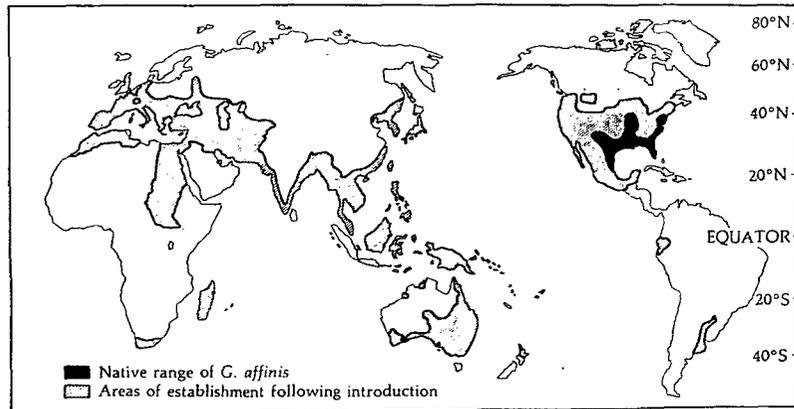


Figure 2.1: Worldwide distribution of *Gambusia affinis*, based on published information and personal communications. Shaded areas indicate that mosquitofish are present in suitable habitats within the region. A full list of references for this distribution map is available on request from the senior author.

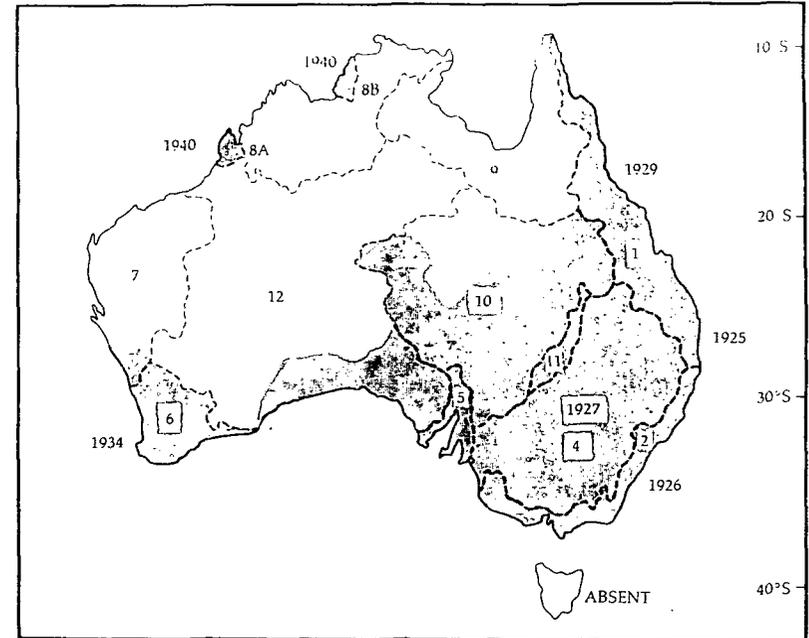


Figure 2.2: Distribution of *Gambusia affinis* in Australia with dates of major introductions. Numbers refer to the drainage divisions recognised by the Australian Water Resources Council.

1. North-east Coast Division
2. South-east Coast Division
3. Tasmanian Division
4. Murray-Darling Division
5. South Australian Gulf Division
6. South-west Coast Division
7. Indian Ocean Division
8. Timor Sea Division
  - A Cape Levesque Coast
  - B Finnis River
9. Gulf of Carpentaria Division
10. Lake Eyre Division
11. Bulloo-Bancannia Division
12. Western Plateau Division

Data on distributions are based on presence of mosquitofish within at least a part of the drainage division. Sources of information are Wilson 1960, Scott et al. 1974; Mees 1977; Lake 1978; McDowall 1980; Glover 1983; Lloyd & Tomasov 1985.

Table 2.1: Schedule of *Gambusia affinis* introductions<sup>1</sup>.

Year	Country, Place	Reference
1905	Hawaii	Seale 1917
1911	Taiwan	Sasa & Kurihara 1980
1913	Philippines	Seale 1917
1916	Japan	Sasa & Kurihara 1980
1921	Spain	Meynell 1973
	Germany	Fowler 1970
	rest of Europe	Krumholz 1948
1922	Italy	Krumholz 1948, Cataudella & Sola 1977
1924	Jugoslavia	Gerberich & Laird 1968
	Canada (Banff)	McAllister 1969, Gerberich & Laird 1968
1925	USSR	Motobar 1978, Sokolov & Chivaliova 1936
1926	Algeria	Gerberich & Laird 1968
	Australia	Wilson 1960
	Corsica	Gerberich & Laird 1968
1927	Italy (2nd attempt)	Krumholz 1948
1928	Greece	Motobar 1978
	Iran	Motobar 1978
	Iraq	Al-Daham et al. 1977
1929	Egypt	Motobar 1978
	Sudan	Motobar 1978
	Thailand	Smith 1945
	Cyprus	Gerberich & Laird 1968
1930	British Solomon Is.	Glucksman & West 1976
	New Zealand	Allen 1956
	Papua New Guinea	Glucksman & West 1976
	West Irian	Glucksman & West 1976
1939 on	Pacific Islands	Gerberich & Laird 1968
1943	Canary Islands	Krumholz 1948, Gerberich & Laird 1968
1956	India	Das & Rampal 1966
1970	Afghanistan	Motobar 1978
Undated	Austria	Fowler 1970
	China	Fowler 1970
	Mexico	Gerberich & Laird 1968
	Morocco	Gerberich & Laird 1968
	South Africa	Fowler 1970, Bowmaker et al. 1978
	Syria	Gerberich & Laird 1968

<sup>1</sup>A complete list of references for this table is available on request to the senior author (L.N.L.).

## Habitat and environmental tolerances

### Habitat

The habitats of endemic mosquitofish are lowland ponds, lakes and streams of south-eastern USA (Casterlin & Reynolds 1977). The species prefers sluggish water,

the shallows and margins of pools, dark-coloured substrates and dense subsurface vegetation, which provides lateral, rather than vertical, concealment from predators (Casterlin & Reynolds 1977). Rapid-flowing waters are avoided, perhaps because predatory efficiency is low, and long-term survival impossible (Reddy & Pandian 1974).

In Australia, mosquitofish occur widely in inland and coastal drainages of slow to moderate flow with variable habitat conditions (Bayly & Williams 1973; McDowall 1980). They have also been found in swamps and lakes, billabongs (Shiel 1980), thermal springs (Bayly & Williams 1973), salt lakes (Chessman & Williams 1974), the cooling pondage of a power station (Cadwallader et al. 1980), and in the ornamental ponds of many urban parks.

Disturbed environments seem particularly susceptible to invasion by mosquitofish and other exotic species (Courtenay et al. 1974; Moyle 1976). In urban Brisbane, the proliferation of *G. affinis* has coincided with modifications to stream channels resulting from construction of water-supply dams and flood retention basins, diversion of stream channels for flood mitigation, excavation of sand and gravel, and the building of bridges and freeways (Arthington et al. 1983). Mosquitofish are particularly abundant in stream reaches bordered or overgrown by para grass (*Brachiaria mutica* [Forssk.] Staph), an aggressive, introduced species which invades the free water, significantly reducing current speeds and the extent of open water (Ham 1981; Arthington et al. 1983). *G. affinis* is found predominantly at the margins of pools with little or no flow, amongst para grass and sedges which provide protection from predatory fishes and birds and from the full force of flood waters.

### Temperature tolerance

Mosquitofish are naturally eurythermal (Falke & Smith, 1974), tolerating temperatures from 0.5°C to 38°C (Otto 1973) or even higher for short periods. Females show more resistance to high temperatures than males, and smaller (hence younger) individuals are more resistant than larger individuals (Winkler 1975, 1976; Johnson 1976a). Diel variation in heat resistance occurs, with maximum resistance at midday (1000–1400 h; Johnson 1976a). Diel variations reflect acclimation effects due to the total diel temperature cycle rather than to the maximum temperature experienced (Winkler 1975). Mosquitofish show a thermal preference for water of 31°C and thermoregulate, during the day, by moving from deep to shallow water (Winkler 1979).

Thermal tolerance and thermal preference in *G. affinis* are stable physiological characteristics under genetic control. Exposure of populations to heated effluents (up to 50°C) for ten years has less effect on the maximum temperature tolerated than acclimation (Smith & Harvey 1974). Cold-adapted and warm-adapted populations have very similar high and low temperature tolerance (Otto 1973), although there is a slight shift in the range of temperatures tolerated. No genetic basis for these shifts has been established.

Wide thermal tolerance and the ability to survive in environments which temporarily exceed the thermal boundaries have many ecological implications for mosquitofish. They allow *G. affinis* to colonise environments at latitudes between 55°N and 44°S, a vast expansion of the native range (see figure 2.1). Exploitation of high temperatures presumably maximises growth, reproduction and population turnover, as in other species (Spieler et al. 1977), and high rates of population growth increase the potential rate of adaptation to new environments (Ferens & Murphy 1974). Because young *G. affinis* are more resistant to high temperatures than adults, they can exploit warm patches of the environment, in particular the shallow edges of pools. When these are vegetated, they offer protection from predators (Barney & Anson 1921), as well as from cannibalism by adults.

Wide thermal tolerances also allow the exploitation of thermally altered environments (e.g. rivers receiving heated water and wastes) without competition from other species (Winkler 1976). Indeed, mosquitofish are sometimes the only fish found in such systems (Aho et al. 1975).

### Salinity tolerance

Mosquitofish occur in freshwater lakes and streams, in the brackish water of estuaries (Stearns & Sage 1980) and salt lakes (Chessman & Williams 1974). They are generally restricted to field salinities of less than 25 g l<sup>-1</sup> (Walters & Legner 1980), but have been found in an Australian lake with salinities in excess of 30 g l<sup>-1</sup> (Chessman & Williams 1974). In the laboratory the LC<sub>50</sub> for salinity has been measured as 58.5 g l<sup>-1</sup> (Chervinski 1983).

### Dissolved oxygen tolerance

Mosquitofish survive oxygen depletion which causes heavy mortalities in other teleost species (Kushlan 1974). Because of their dorsally oriented mouth and flattened head, they can utilise the surface film of water, which is rich in oxygen even in otherwise anoxic situations (Lewis 1970). The 96 h LC<sub>50</sub> for oxygen is approximately 0.2 mg l<sup>-1</sup> (Sjogren 1972) if fish are given access to the surface. Complete survival has been observed for mosquitofish, without access to the surface, at oxygen concentrations of 1.3 mg l<sup>-1</sup> (Odum & Caldwell 1955).

### Tolerance to pollutants

*G. affinis* is resistant to a wide variety of pollutants, including organic waste, heavy metals, insecticides, herbicides, rotenone, phenol and radiation (table 2.2). Mosquitofish thrive in sewage oxidation ponds (Fisher et al. 1970) and have been reported from a stream polluted by paper-mill effluent, although this induced non-functional gonopodia in females and precocious sexual maturation and behaviour (Howell et al. 1980).

Table 2.2: Tolerance of *Gambusia affinis* to selected pollutants.

Pollutant	Concentration		Comments	Source		
Mercury	0.005 ppm over 24 h		Sub-lethal dose. No effect on escape behaviour. Sub-lethal doses: increasing alteration of escape response with high concentrations.	Kania & O'Hara 1974		
	0.01 ppm over 24 h 0.05 ppm over 24 h 0.10 ppm over 24 h					
Insecticides	48 h LC <sub>50</sub> (ppb)		Many of these insecticides are used in mosquito and general insect control. The resistant strain of fish had been exposed to most of these insecticides for many years previous to testing.	Culley & Ferguson 1969		
	Susceptible strain	Resistant strain				
DDT	19	96				
Dimite	3094	3872				
Methoxychlor	109	186				
Perthane	479	1542				
Kelthane	777	2121				
Eldrin	0.6	314				
Strobane	11	6253				
Heptachlor	35	12500				
Toxaphene	12	4519				
Chlordane	41	3804				
Aldrin	36	2558				
Dieldrin	8	434				
Lindane	74	3104				
Ethion	206	983				
TEPP	2845	3500				
Phosdrin	2914	2935				
Malathion	1061	841				
Parathion	48	199				
Methyl trithion	720	1078				
Ronnel	1450	1753				
Methyl parathion	4000	-				
Dursban	1018	1291				
Guthion	68	79				
CO-RAL	3500	-				
Herbicides	48 h LC <sub>50</sub>					Johnson 1978
Fenoprop	0.52 ppm					
Sodium arsenite	100 ppm					
Picloram	125 ppm					
MSMA	186 ppm					
2, 4-D amine	445 ppm					
Dicamba	510 ppm					
Paraquat	751 ppm					
DSMA	1.4 g l <sup>-1</sup>					
2, 4, 5-T amine	2.5 g l <sup>-1</sup>					
Amitrole-T	3.1 g l <sup>-1</sup>					
2, 2-DPA	23.1 g l <sup>-1</sup>					

(cont. page 14)

Pollutant	Concentration		Comments	Source
Rotenone	24 h LC <sub>50</sub>		Resistant strain developed resistance without exposure to rotenone.	Fabacher & Chambers 1972
	Susceptible strain	Resistant strain		
	0.017 ppm	0.031 ppm		
Phenol	24 h LC <sub>50</sub> 75 mg l <sup>-1</sup>			Meynell 1973
Gamma radiation	LD <sub>50</sub> over 30 days 3699 rads (at 25° C.)		Fish more sensitive to radiation at higher temperatures.	Blaylock & Mitchell 1969
Ionizing radiation	10.9 rads day <sup>-1</sup>		Sub-lethal; higher than normal embryo mortality and deformity.	Blaylock 1969

Pesticide tolerance and resistance have been intensively studied, as mosquitofish are used in combination with pesticides to control mosquito larvae in American rice fields. Populations resistant to particular pesticides are often resistant to other pesticides without prior exposure (Kynard 1974; McCorkle et al. 1979). However, selection for pesticide resistance is not accompanied by increased resistance to other environmental stresses (McCorkle et al. 1979). For instance, lower tolerances to oxygen and temperature stress may result from exposure to pesticides (McCorkle et al. 1979).

Mosquitofish are tolerant of a number of heavy metal pollutants (zinc, selenium, copper, arsenic, mercury and uranium) and live in concentrations lethal to other species (Cherry et al. 1976). They survive when exposed to daily radiation levels of 10.9 rads, although mortalities and abnormalities of embryos are increased (Blaylock 1969). Temperatures above 20°C cause increased radiosensitivity (Blaylock & Mitchell 1969).

## Reproduction and development

Female *G. affinis* employ single-brooded ovoviviparity, producing successive broods of moderate-sized young that are nourished by yolk, with minimal dependence on maternal nutrients (Chambolle 1973; Thibault & Schultz 1978; Miller 1979). The gestation period is relatively short compared with other Poeciliidae, varying from 21 to 28 days at 25°C (Krumholz 1948), although Hildebrand (1917) recorded brood intervals of 16–43 days (mean 29.2 days) and brood intervals of 28–140 days have been observed in Western Australian populations (Trendall 1982). Fry are 5–8 mm long at birth and grow quickly at first, but the growth rate is variable, depending on temperature (Johnson 1976b), food supply (Krumholz 1948; Goodyear et al. 1972), and space (Reddy & Katre 1979).

Female *G. affinis* usually mature when 4–6 weeks old at standard lengths of 18–20 mm (Krumholz 1948; Brown & Fox 1966; Sawara 1974; Milton & Arthington 1983). Senility of the female reproductive organs occurs, but depends on the age of first attaining sexual maturity; females which mature early become senile early (Krumholz 1948). Males become mature at 17–23 mm standard length when as young as 4 weeks old (Krumholz 1948; Ham 1981; Trendall 1982). Growth practically ceases after the gonopodium of the male is completely formed (Krumholz 1948). Thus adult males exhibit a narrow size-range in most populations (17–30 mm). Exceptional males may reach 38 mm and females 65 mm (Brown & Fox 1966). Early maturing fish usually die before their first winter, but those which do not mature until after their first winter may survive up to their third summer (Krumholz 1948).

The seasonal timing of the reproductive cycle in *G. affinis* is governed primarily by photoperiod, modified by temperature (Brown & Fox 1966; Sawara 1974; Davis 1978). Brown and Fox (1966) show that reproduction ceases when day length falls below 12.5–13 h, even though water temperatures remain favourable. In Brisbane, *G. affinis* begins to breed in early August following an increase in photoperiod beyond 11 hours, at water temperatures of 17–18°C during the day (Milton & Arthington 1983). Disparities of this kind suggest differences between the subspecies or between populations in sensitivity to photoperiod (Sawara 1974).

The length of the reproductive season varies with latitude. At high, northern latitudes, it may extend from May to September (Sawara 1974), in northern mid-latitudes (i.e. the native range) from February to October or December (Davis 1978), and year-round in the tropics (Martin 1975; Motobar 1978). The reproductive season in Western Australia (Perth) extends from November to March (Trendall & Johnson 1981), and in south-eastern Queensland from early August to March, or early April, depending upon the particular stream inhabited (Milton & Arthington 1983; Ham 1981).

Reproductive effort varies throughout the breeding season, with a peak occurring early in the season. Thus, in October in Brisbane, 94 per cent of females are pregnant and produce the largest broods (Milton & Arthington 1983). In males, the breeding peak coincides with the highest frequency of copulation (Geiser 1924).

The fecundity (i.e. brood size) of individual females increases linearly with length and weight and is affected by the trophic status of the environment (Krumholz 1948; Wu et al. 1974; Milton & Arthington 1983). Maximum brood size varies widely and may be as high as 428 young (Motobar 1978), although the average fecundity is 30–50 (Barney & Anson 1921; Krumholz 1948). In Brisbane, the average brood size is 22.78 (range 3–108) in females of 30 mm standard length (Milton & Arthington 1983). Populations from Perth produce 18–31 young per brood in females of 32 mm standard length (Trendall 1982). Assuming that most females breed for one season only (cf. Krumholz 1948), the lifetime fecundity of the species in Brisbane will be around 205 (9 × 22.78) offspring.

Trendall (1982) has recorded substantial variation in life-history traits among four populations of *G. affinis* from Western Australia. Such flexibility in adap-

tive responses of the life history to environment may be an important aspect of the species' ability to colonise new areas and environments disturbed by man.

## Population ecology

Mosquitofish populations may increase very rapidly. For example, Goodyear et al. (1972) cite a tenfold increase in population numbers in only ten weeks. Maglio and Rosen (1969) suggest that, under ideal conditions, ten pregnant females, along with subsequent offspring, might produce as many as 5 million fish in six months. Densities of up to 30 000 mosquitofish ha<sup>-1</sup> have been recorded in American rice fields (Hoy & O'Grady 1971; Reed & Bryant 1974). However, the dynamics of mosquitofish populations are poorly documented, despite the wide use of the species. Individuals do not interchange between populations on a large scale (Martin 1975; Goodyear 1973), and because of this, populations tend toward lowest densities through winter and autumn, when reproductive effort is low and mortality is high. Conversely, highest densities occur in late spring and summer (Krumholz 1948; Martin 1975; Kushlan 1980; Ham 1981; Milton & Arthington 1983).

Predation, principally by other fish, removes the aged, senile individuals in populations of *G. affinis* (Sohn 1977). In Australia, important fish predators include species of *Anguilla*, *Mogurnda*, *Gobiomorphus*, *Leiopotherapon* and *Glossamia*, but their impact on mosquitofish populations has not been studied. However, Arthington et al. (1986) have studied prey selection by *Glossamia aprion* (Richardson) in aquarium experiments with *G. affinis* and other species. When the numbers of each prey species were equal, the smallest fish were eaten first, regardless of their identity. Extrapolating these observations to the field, selective predation by piscivorous fish may explain the observed numerical dominance of *Xiphophorus helleri* (Günther) (the larger of these two exotic species) over *G. affinis* in areas of coexistence. In the absence of predatory fish, *G. affinis* is almost always more abundant than *X. helleri* (Arthington et al. 1986).

Piscivore avoidance involves a complex of behaviours. Mosquitofish from populations exposed to predators use a sun-compass orientation to return quickly and accurately to their home shore (Goodyear & Ferguson 1969). Shoreward orientation is more accurate in younger fish and is reinforced by predator pressure. Fish which encounter a predator exhibit a fright response, remain motionless, then move quickly to the home shore (Goodyear 1973).

Various birds prey on mosquitofish and the snowy egret (*Leucophoyx* sp.) has even developed a bill-vibrating behaviour pattern that attracts its prey (Kushlan 1973). Species of the predatory water spider, *Dolomedes*, are capable of catching and eating mosquitofish (Suhr & Davis 1974; Williams 1979).

Parasites of mosquitofish include the glochidia of freshwater mussels (D'Eliscu 1972; Stern & Felder 1978; Walker 1981), brain and body-cavity parasites (Aho et al. 1975), and a protozoan parasite causing ovarian atrophy, reduced fecundity and, ultimately, death (Crandall & Browser 1982).

*G. affinis* is an aggressive fin-nipper (McDowall 1980) and, at times, a piscivore (Myers 1965) which also cannibalises its fry. Johnson (1976b) found that adults consumed  $2.66 \pm 0.27$  fry per day in clear water. Differential utilisation of habitats and food resources probably reduces cannibalism and intraspecific competition in *G. affinis*. In Brisbane, juveniles are largely confined to shallow, open water with no flow, vegetated areas, debris and overhanging banks, whereas larger fish occupy a wider range of habitats (Ham 1981).

Mortality rates in *G. affinis* populations in response to physico-chemical factors are virtually unknown. Krumholz (1948) and Winkler (1975) noted that temperature extremes cause differential death of males and large females. The frequency of vertebral anomalies of fry increases with temperature, as does the number of dead embryos per brood caused by heat stress *in utero* (Winkler 1976). Some internal parasites of mosquitofish also benefit from high temperatures (Aho et al. 1975). Natural mortality of mosquitofish seems to vary according to algal density and turbidity during the first few days of life, but not thereafter (Johnson 1976b).

## Diet

*G. affinis* is an omnivore with a preference for animal food (Al-Daham et al. 1977; Farley 1980). Zooplankton, drifting invertebrates, insects that fall on the water's surface, and certain benthic invertebrates are the major constituents, with mosquito larvae often comprising only a minor part of the diet (Farley 1980; Grubb 1972; Walters & Legner 1980; Whitaker 1974).

In Australia, Cadwallader (1979) found that *G. affinis* from the lower reaches of the Seven Creeks River System in the Murray-Darling Basin consumed larval Diptera and Trichoptera, adult Coleoptera, spiders, and various terrestrial insects; over 80 per cent of the food items in mosquitofish guts were terrestrial insects. Mosquitofish generally select the largest prey they can successfully capture (Wurtsbaugh et al. 1980), presumably to optimise net energy gain.

## Effectiveness in mosquito control

Many workers have noted that mosquito larvae generally make up only a small part of the diet of *G. affinis*. Indeed, mosquitofish may suffer heavy mortalities when fed exclusively on mosquito larvae, and the survivors show poor growth and delayed maturation (Reddy & Pandian 1972). Although presumed to be effective in mosquito control, few rigorous tests have been done. At low densities, *G. affinis* may encourage mosquito larvae by preying on their invertebrate predators (e.g. odonates and notonectids; Stephanides 1964; Hoy et al. 1972; Walters & Legner 1980; Hurlbert & Mulla 1981). Other studies have shown that as many as 5000 fish ha<sup>-1</sup> would be required for effective larval control (Davey & Meisch 1977).

In Australia, there are three distinct mosquito problems, domestic, freshwater and saltwater, each caused by different species (Kav et al. 1981). Some of the most important biting pests and vectors of disease are little affected by fish because of the temporal and spatial patchiness of their breeding environments, e.g. *Culex sitiens* Wiedemann, *C. fatigans* Wiedemann, *C. annulirostris* Skuse, *Aedes vigilax* (Skuse), *A. normaniensis* (Taylor), *A. notoscriptus* (Skuse) and *A. aegypti* (L.). Although *G. affinis* is reported to exert good mosquito control in permanent swamps and pools (see Wilson 1960), this has not been substantiated.

Many fisheries biologists believe that native fish such as the hardyheads (*Craterocephalus*), smelt (*Retropinna*), rainbowfishes (*Melanotaenia*), gudgeons (*Hypseleotris* and *Mogurnda*) and *Galaxias* are equally, or more, effective as mosquito predators than is *G. affinis* (see McDowall 1980; Lloyd 1984). Unfortunately, the impact of native fish has not been determined experimentally and there are few published accounts of their value in the field. Nevertheless, it is hard to make a strong case for the continuing use of *G. affinis* for mosquito control. If there are outstanding examples of the species' contribution to mosquito control in Australia, these are not documented. However the environmental impact of *G. affinis* is now the focus of concern (Stephanides 1964; Tabibzadeh et al. 1970; Hurlbert et al. 1972; Smith 1973; Motobar 1978; Schoenherr 1981).

## Environmental impact

The impact of *G. affinis* on aquatic environments was a minor concern (Barney & Anson 1921) before worldwide distribution of the species began. Later, field observations reinforced the belief that the mosquitofish has destructive effects on invertebrate populations (Stephanides 1964; Legner & Medved 1974). Controlled experiments support these observations, showing substantial impact on beetles (Walters & Legner 1980), back swimmers (Hurlbert & Mulla 1981), rotifers, crustaceans (Hurlbert et al. 1972) and molluscs (Rees 1979).

According to Myers (1965), mosquitofish have wiped out most native larvivorous fish almost everywhere they have been introduced, as well as taking a heavy toll of the fry of larger species. Schoenherr (1981) claimed that at least 25 species in many parts of the world have been affected by *G. affinis*. When hybridisation or direct predation is not involved, interspecific competition is usually implicated (e.g. Deacon & Bradley 1972; Cross 1976).

Mosquitofish may also threaten native species by predation on their eggs and fry and by nipping the fins of adult fish, leading to fungal infections and death (McKay 1984). Lastly, mosquitofish exposed to pesticides may develop resistance and replace native fish which are less tolerant (Moyle & Cech 1982).

In Australia, the evidence for adverse impacts of mosquitofish on native fish is patchy and mostly circumstantial (see Marshall 1966; Reynolds 1976; Cadwallader 1978; Lake 1978; Wharton 1979; McDowall 1980; McKay 1984). *G. affinis* has been implicated in the decline of the purple-spotted gudgeon,

*Mogurnda adspersa* (Castelnau) (Hoese et al. 1980), and species of *Melanotaenia*, *Ambassis*, *Pseudomugil*, *Craterocephalus* and *Retropinna* in Queensland (Arthington et al. 1983) and elsewhere (Marshall 1966; Mees 1977; Lloyd 1984). However, habitat destruction and water-quality degradation have also reduced native fish populations (Arthington et al. 1983). Irrespective of man's involvement in the decline of native fish, *G. affinis* is a pest in Australia. Its importation is illegal, and some states have declared it a noxious species, prohibiting its use in mosquito control.

## Conclusions

*G. affinis* is a ubiquitous, introduced fish which has been distributed worldwide as a mosquito-control agent. It is eurytopic, occurring even in heavily polluted habitats. Its reproductive behaviour and flexible life history may be a key to understanding why it has become established in aquatic systems affected by unpredictable human disturbances. Rapid maturation, the production of moderate-sized broods at frequent intervals, with the peak of reproductive effort early in the season when food is abundant, all tend to increase the rate of population growth, regardless of female survivorship. Flexible behaviour patterns, omnivory, strong competitive ability and wide environmental tolerances also contribute to the species' success.

Man has been partly responsible for the success of *G. affinis* by assisting in the species' large-scale dispersal. However, unlike many other species of introduced fish, mosquitofish will thrive in natural and altered aquatic systems without the intervention of man.

*G. affinis* is still used in mosquito control, but there is mounting evidence that it is often relatively ineffective. Native predacious fish probably contribute to mosquito control in many parts of the world. In Australia, several potentially useful native species have become rare where mosquitofish are abundant. Deliberate, further spread of *G. affinis* should be prohibited.

There is now sufficient information on the biology and ecology of the mosquitofish to permit a shift from basic studies to critical research directed towards understanding impacts on native fish and aquatic ecosystems. Work on feeding preferences of native species, the role of habitat structure, and detailed information on foraging will be particularly apposite.

## Acknowledgments

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